

Chapter 9 Effects of management on vegetation structure

Having discussed the effects of microclimate and vegetation structure on the flora and fauna, it is important to outline to various ways in which vegetation is managed. The management options include grazing (its timing, intensity, and type of grazing animal), mowing, burning and herbicides which are mainly concerned with the management for a particular vegetation structure. Hence, management for invertebrates is considered separately in terms of the effects of grazing, cutting, fire and variations in their timing and intensity.

9.1 Introduction

Herbaceous vegetation in Britain is of considerable importance for the conservation of wildlife and landscape and embraces a wide range of plant communities. These range from species-rich limestone grasslands, over calcareous rendzina soils, to species-poor heathlands over acidic podsols. They are semi-natural communities, being on land cleared from forest by man and maintained by his stock. Many of their constituent species are from continental ecosystems, most, like the early spider orchid (*Ophrys sphegodes*) and the Dartford Warbler (*Sylvia undata*), being rarities which gain only a slender foothold in the British Isles (Green, 1983).

The Nature Conservancy Council (1984) estimated that between 1949 and 1984: 80% of limestone grasslands, 40% lowland heathlands, 50% lowland wetlands and 30% upland moors were lost or significantly damaged. Overall, as a result of habitat losses and fragmentation, 10 species of flowering plant, 3-4 species of dragonfly and one species of butterfly have become extinct in Britain. In addition, 149 plants, 13 butterflies, 11 dragonflies, 4 reptiles and amphibians, 36 birds and several mammals, now have seriously declining, or endangered populations (Green 1990). Many of these are species of grassland which supports a substantial proportion of the total British flora and fauna. On remaining grasslands, the loss of traditional management (abandonment) and intensification of farming have both led to species losses. On the six main heathland areas in southern Britain, the total extent has decreased from 143, 250 ha in 1830 to 29, 450 ha in 1980, a decrease of 72% (Nature Conservancy Council, 1984). Most heathland has been lost through conversion to pasture or arable land, afforestation or used for building. Losses through lack of grazing, or similar neglect, have been small. More important has been the

effect of fragmentation and isolation of the remaining heathland on rare plant and animal species.

Grasslands and heathlands are plagioclimax communities only maintained by external agencies such as grazing, mowing, and burning which prevent natural succession to scrub and finally woodland. Harvesting material from ecosystems has two main effects: disturbance and nutrient impoverishment (Green, 1986), which both favour species of open swards rather than colonisers. Woody species with their growing points in exposed apical buds are constantly suppressed by disturbance, allowing grasses and rosette herbs with growing points at, or below, ground level to persist. The vegetation and soils of limestone grasslands and heathlands are very impoverished in nitrogen and phosphorus (Green, 1972). More vigorous, nutrient-demanding species are constrained, allowing a wide range of the typical slower-growing and less demanding grasses and herbs to flourish.

9.2 Grazing

This is often regarded as the best way of maintaining most kinds of herbaceous swards, particularly grasslands. In considering the use of livestock, attention must be paid to the objectives for the site, the former management history, the suitability of different types of stock, the desirability of extensive or rotational grazing, stock husbandry requirements and overall control of grazing (Bacon, 1990). Departures from the traditional management of a site should not be made without good reason, since distinct (i.e. 'typical') botanical and invertebrate communities develop in relation to particular management regimes. Good grazing management depends on control of three main variables: 1. time of year at which grazing takes place, 2. intensity of grazing and 3. type of stock/grazing animals used.

9.2.1 Time of year at which grazing takes place

The season of grazing is important for management, because defoliation removes leaves, buds, flowers or seeds according to the phenology of each species (Duffey, 1981). It depends on the productivity of the grassland and its previous grazing history. Winter grazing adequately controls herbage growth on low productivity grasslands, whilst avoiding the problem of stock eating flowers (Floyd, 1965). It controls grass species of high competitive ability without affecting the dicotyledon species (and associated insects) which are dormant during this period (Wells, 1974a; Nature Conservancy Council, 1982). The action of animal hooves may be

beneficial by breaking up plant litter and exposing bare ground for colonization, but care must be taken to avoid poaching. Winter grazing is a practical proposition only in the lowlands, but even then supplementary feeding may be needed.

On moderately productive sites, with an earlier start and later finish to the growing season, the period of winter grazing needs to be extended to include either or both of April/May (to control dominant, unpalatable grasses) and September (less harmful to invertebrates, Brown *et al.*, 1990). Annuals, such as Linum catharticum (purging flax), Euphrasia nemorosa (eyebright) and Crepis capillaris (smooth hawksbeard), increase in calcareous grasslands heavily grazed during the winter and spring period (Wells, 1974a). On deeper, more fertile soils swards containing a higher proportion of vigorous grasses may require grazing throughout the summer months, but its intensity should be kept low in order to maintain the botanical interest. Summer grazing may also control the invasion by seedlings of shrub species or scrub regrowth (Floyd, 1965).

9.2.2 Intensity of grazing

Agricultural grassland management aims to maximize production and is concerned with 'grazing pressure', the relationship between the amount of plant material available and the requirement of the animal population (Spedding, 1971). In contrast, conservation management aims to create a particular type of vegetation using the required intensity of grazing in terms of both number of animals and duration. The more animals that are put on a given area of grassland, the more quickly they will produce a sward of even height with little variation in structure. The response of vegetation will vary with its productivity and (life-form) structure. On areas of low productivity, plants are often much less resilient to grazing and may be seriously damaged by a short period of heavy grazing. The 'blitz' graze is also very harmful for invertebrates, especially those dependent on the structure of the sward throughout their life-cycle. In abandoned heathlands, light grazing rejuvenates the heathland vegetation, but heavy grazing greatly increases invasion by grassland species (Bakker, 1978). Unlike lowland grassland, heathland does not recover from winter trampling (Harrison, 1981)

9.2.3 The type of grazing animal used

The choice lies between sheep, cattle, or a combination of both. Ponies are not recommended because of their very selective grazing habit and tendency to dung repeatedly in the same area (Odberg & Francis-

Smith, 1976, 1977), causing local nutrient enrichment (Archer, 1973; Edwards & Hollis, 1982).

Sheep are generally regarded as the traditional grazing animal in chalk grasslands. Their nibbling mouth-action causes the herbage to be grazed very short, often right back to the rootstocks. They graze selectively and may produce distinct botanical communities. At low stocking rates, they will graze the sward between the flower-stalks, thereby protecting the supply of nectar for insects and seed for future years (Nature Conservancy Council, 1982). The most successful breeds for conservation management work are the 'hardy' types, e.g. Welsh Beulah, Welsh mountain, Cotswold. Hill breeds of sheep tend to sleep and dung in the same place every night (Taylor *et al.*, 1987). This can lead to very localised nutrient enrichment, especially when sheep are confined to small compartments (Hilder & Mottershead, 1964).

Cattle (and ponies) are ideal on high productivity sites to remove long or rank vegetation (or scrub), such as tor grass (Brachypodium pinnatum) fairly quickly (Nature Conservancy Council, 1982). Using a 'wrap-around-and-pull' action of the tongue, they are relatively unselective grazers. They may create a mosaic of short grassland interspersed with taller patches (Regnell, 1980; van den Bos & Bakker, 1990). Their hoof action can provide beneficial breaks in the turf (e.g. for butterflies, Thomas, 1983a), provided this does not develop into large-scale poaching which can lead to infestations of Cirsium spp. (thistle) and Senecio jacobaea (ragwort). They also cause erosion on steep slopes and sink into the ground in wet conditions (Nature Conservancy Council, 1982).

Despite being an attractive feature of the English countryside since ancient times, deer grazing is unlikely to be used for conservation due to the high cost of perimeter fencing (Wells, 1980). However, along with goats they may be particularly effective in controlling scrub. Mixed grazing may have distinct advantages and often removes many of the disadvantages of single species grazing, e.g. sheep remove the unsightly ring of herbage around cow-pats and check the growth of ragwort (Nature Conservancy Council, 1982).

9.3 Cutting

This heading could include the turf-cutting and sod-cutting (Werger & Prentice, 1985) practised in some grasslands and heathlands respectively. However, this section concentrates on the mowing of grasslands. This is

another method of defoliation suitable for sites which are small or inaccessible for sheep grazing, e.g. road verges (Melman *et al.*, 1988). It can also be used to increase diversity by controlling vigorously growing species, e.g. Brachypodium pinnatum (tor grass) in chalk grasslands (Wells, 1965; Bobbink & Willems, 1991), Arrhenatherum elatius (false oat-grass) in dunes (Hewett, 1985). Wells (1971) showed that cutting is an effective substitute for sheep grazing on chalk grassland, since it led to no loss of species but produced a different balance in the vegetation. However, cutting differs from grazing in three respects: 1. It is non-selective, all vegetation above the blade being severed. 2. It makes it possible to remove nutrients in the form of hay as well as returning them as 'clippings'. The latter has similar effects to animal excreta, i.e. it smothers vegetation preventing light penetration and fertilises the soil. This may reduce floristic diversity (Parr & Way, 1987) 3. It does not exert the same localised pressure as hooves (Wells, 1980).

Plants commonly found in hay meadows are adapted to cutting but can not withstand grazing, e.g. Arrhenatherum elatius (false oat grass), Bromus commutatus (meadow brome), and Sanguisorba officinalis (great burnet) are absent from Port Meadow but abundant on Pixey and Yarnton Meads, the former grazed and the latter cut for hay since 1085 (Baker, 1937). The reproductive processes in meadow plants are closely related to the type of management under which the plant community has evolved (Wells, 1974b). The timing of year and frequency are the most important ways of manipulating cutting in grasslands. Bobbink *et al.* (1987) showed that mowing earlier in the year resulted in a reduced exclusion of species by Brachypodium pinnatum (tor grass).

9.4 Burning

9.4.1 Grasslands

Fire is an important ecological factor in many of the world's grasslands (Daubenmire, 1968), particularly in semi-arid regions, but may also be used as a management tool in the reclamation of unmanaged grassland or as part of a rotational system (Wells, 1980). Burning is a valuable method of destroying the dense mattress of dead grass leaves so often found at the base of ungrazed chalk grassland (Wells, 1965, 1974c). Grass litter is broken down only slowly and tends to accumulate and 'smother' many low-growing species. In the Cotswolds and Peak District of Derbyshire considerable areas are burnt ('swaled') annually (February-early March) to control the coarse grasses, Brachypodium pinnatum (tor

grass) and Bromus erectus (upright brome) and checking scrub invasion (Lloyd, 1968). An important effect of fire is the creation of small areas of bare ground between tussocks. These provide ideal conditions for the establishment of many grassland plants, both perennial and annual. Annuals, such as Linum catharticum, invariably increase during the first and second year following fires and subsequently decrease if fires are prevented. Inflorescence production may also increase in the year following a fire (Lloyd, 1968).

9.4.2 Heathlands

Burning is the most effective method maintaining lowland heathlands and aims to prevent invasion of scrub, trees and bracken and produce, by rotational management, a mosaic of ericaceous vegetation of different ages, representing the entire growth cycle of Calluna. In contrast to the management of upland moors for grouse on a 10-12 year rotation (Gimingham, 1972), lowland heathlands are managed for conservation on a 15-20 or even 30 year cycle (Webb, 1986). The heathland is usually broken up into plots of up to 2 ha. each, preferably surrounded by older heather which acts as a source of colonists. Many small heathlands of less than 5 ha are very difficult to manage since there is an insufficient area to maintain a rotation and an inadequate source of colonists.

Due to the inflammable nature of heather, burning is prohibited between 31 March and 1 November without a special license although for most of the winter the vegetation is too damp. The best period is usually from mid-February to late March, when frosts and wind have dried the vegetation and before the new flush of spring growth commences. Heather can only be burned when the wind is light and a break of 5 m must be cut round the area to be burnt. The aim is to remove all the above-ground vegetation cleanly yet leave the roots unharmed for regeneration. This can only be achieved when the intensity of the fire is carefully controlled. The best results are obtained when the fire is allowed to burn against the wind ('back-burning') and it is easier to control both the intensity and speed with which the fire moves through the vegetation. If a fire is allowed to burn with the wind the result is often poor, because much of the material remains unburnt.

The periodic burning of heathland has two important effects: it modifies the structure of the vegetation and it ensures that the nutrient status remains low. The intensity of the fire varies depending on the wind strength, direction and force, and on the age and moisture content of the vegetation and this may influence the succession which follows. Using heat-

sensitive paints, Whittaker (1961) found that at ground level temperatures were in the range 300-500 °C, while in the canopy they reached 840 °C. Similar temperatures were found by Kenworthy (1963) using thermocouples. The duration of high temperatures increases with stand age reflecting the quantity of fuel available.

The fire may modify regrowth of Calluna in two ways: by affecting regeneration of the rootstock, or, if the roots have been killed, by affecting germination of buried seed in the soil. If the stem bases are exposed to temperatures higher than 500 °C for more than one minute, they may be killed (Whittaker, 1961). Calluna plants decline in their ability to regenerate with age (Mohammed & Gimingham, 1970; Miller & Miles, 1970) and the season of burning is also important. If a stand is young, regrowth is mainly vegetative, but seedling regeneration becomes increasingly important when older stands are burned (Hobbs & Gimingham, 1984) or where a fire has got out of control and produced excessive heat. Whittaker and Gimingham (1962) found that seeds of Calluna were killed by charring and exposure to 200 °C or lower temperatures for longer periods.

Large numbers of seeds of Calluna (Miller & Cummins, 1987) are present in the soil beneath heathlands and these may retain viability for several years. The amount of seed stored in the soil declines with age of the stand for most species, but for Calluna it increases with age. The richest flora regenerates when the youngest stands are burnt, and declines with the pre-burn age of the stand. There is a well developed sequence of plants colonizing freshly-burnt heath, each with different life-cycle strategies. Lower plants (i.e. lichens and bryophytes), grasses (e.g. Molinia caerulea), dwarf gorses (Ulex minor and U. gallii) and bracken (Pteridium aquilinum) are conspicuous in the early-post fires stages. The rate at which these secondary successions take place is determined by the rate of regeneration by Calluna, and this in turn is influenced by the age of the stand before burning (Hobbs *et al.*, 1984), the intensity of the fire and the environmental conditions (e.g. soil fertility) before and after burning.

Vegetation changes also occur in the absence of burning, notably in the direction of scrub invasion (Harrison, 1981). There are two stages in heathland development where tree seedlings may become established. Firstly, when the cover of Calluna is low during the first five or six years after fire birch (Betula spp.) and pine (Pinus sylvestris) seedlings may take advantage of these environmental conditions (Marrs, 1987b). Secondly, establishment can occur when Calluna plants enter the degenerate phase at around 15 years old and the canopy begins to open out again. Without

appropriate burning or other management (e.g. grazing, scrub cutting, herbicides, Marrs, 1987a) to maintain vigorous growth of Calluna, losses of open heath communities may occur through successional change towards woodland (Marrs et al., 1986).

9.5 Herbicides

In grasslands, these may be used in the spot treatment of noxious weeds such as creeping thistle (Cirsium arvense) and broad-leaved dock (Rumex obtusifolius) (Wells, 1989) and growth retardants have been employed on roadside verges to control grasses and maintain diversity (Parr & Way, 1988). In areas where dense thickets of scrub exist and the ground layer is poor, cutting of scrub by hand followed by the chemical treatment of stumps produces beneficial results. In some cases, drastic measures, such as winching out of scrub, followed by rotovation or ploughing may be needed (Ward, 1974).

Birch, pine and Rhododendron have invaded lowland heathlands because fire has not controlled them and grazing has ceased. Scrub can be controlled by a combination of cutting and/or spraying with herbicides (Marrs, 1985). Although herbicides are a potent and cost effective tool, there is resistance to their use since there may be adverse long-term effects. Bracken is another invasive species and can be similarly controlled. Cutting should take place when the reserves of food in the rhizome are lowest, from mid-June to late July. The effect of the herbicide Asulam depends on initial frond density and the type of stand (Webb, 1986).

9.6 Management for invertebrates

Invertebrate species of grassland are dependent on three components of a ecosystem: the grazing animals, particular plant species and the gross structure of the vegetation. The former provides 'vertebrate products' including the living animal (i.e. parasites and parasitoids), carrion (flesh, bones, fur and wool), dung, discarded fur and wool and 'animal artefacts' (rabbit burrows, Morris, 1969). Almost every structural component of grassland plants is exploited by herbivorous invertebrates. A distinction can be made between the structural differentiation of individual plants and the over-all, gross structure of the vegetation. Particular plant species may contain specialists on their roots, leaves, stems, buds, flowers, fruits and seeds (Duffey, 1983). The quantity and quality of these resources may be

altered by management, e.g. the intensity of grazing affects flower production (Morris, 1971b).

The importance of vegetation structure to invertebrate predators has long been recognized (i.e. 'habitat types', Elton & Miller, 1954) e.g. the spider fauna (Duffey, 1962a, b). More recent studies (Morris, 1971b) suggest that there is a general relationship between the height of grassland vegetation and the abundance and diversity of insects inhabiting it at least in certain taxonomic groups, e.g. Heteroptera and Auchenorrhyncha. The importance of stratification in determining the composition and abundance of leafhopper faunas in meadows was shown by Andrzejewska (1965). Morris (1968) found three times as many beetles in ungrazed as on short grazed chalk grassland. Grazing (or mowing) has the effect of reducing vegetation height resulting in a loss of species adapted to both structural 'micro-habitats' in the upper zones (e.g. orb-web spiders, flower- and seed-feeding insects) and to the moist 'micro-climates' of the litter-layer (Waterhouse, 1955) lower down (Duffey, 1983). Tussock formation in intensively grazed grasslands may permit the survival of certain species which overwinter in grasslands (Luff, 1966; Morris, 1971b).

9.6.1 Grazing

Although all methods of management lower the mean height of the vegetation and reduce standing crop, there are important differences between grazing and other methods. Grazing is selective, producing a patchy sward, and this clearly operates against invertebrates associated with palatable plants but allows those feeding on thistles, or similarly defended plants, to survive. The effects of trampling, which breaks up the litter layer and compacts the soil surface, may be considerable (Duffey, 1975). In intensively grazed grasslands, some-ground dwelling invertebrates flourish, but the fauna as a whole is impoverished. The dung of grazing animals provides a habitat which is unavailable under other management methods. Grazing is a more or less gradual process, whereas mowing and burning are sudden and catastrophic.

9.6.2 Cutting

The effects of cutting on invertebrates are similar to those produced by grazing, when allowance is made for the continuous nature of the latter in contrast to the suddenness of the former. At Castor Hanglands N.N.R., on oolitic limestone grassland, Morris (1981a, b) found that 23 species of Auchenorrhyncha were affected adversely by cutting, while only 8 species increased in numbers following treatment. However, intensive grazing

produces a shorter sward than can be produced by cutting. Cutting tends to remove all flowers and seedheads at the time of application, whereas a few survive under grazing because of its selective nature.

9.6.3 Fire

This is the traditional management used to control coarse grasses (e.g. *Brachypodium pinnatum*) in areas such as the Cotswolds. Its effects on invertebrates have been little studied (mainly in N. American prairies, Lussenhop, 1976; Evans, 1984, 1988), but are likely to be extreme though short-lived. Recently-burned grasslands are often tall, with abundant inflorescences, but have little litter or standing crop of foliage and consequently few Auchenorrhyncha, for instance (Morris, 1975). Hot fires, such as those burned against the wind, may kill some sedentary animals, such as snails, which would survive grazing or cutting (Morris, 1990).

Miller (1974) studied the invertebrate fauna in heathlands in relation to the different growth phases of heather. He found that burning resulted in a less diverse fauna in the litter and in the air above the plants, an increase in that on the litter surface, and almost no change in the canopy. In mixed-age stands, there was little difference between the faunas of the patches of plants representing the different phases. However, in managed, even-age stands, although the faunal composition may be similar from phase to phase, densities are highest in the oldest phases. Similar conclusions have originated from studies of individual invertebrate groups (e.g. ants, Brian, 1964; spiders, Merrett, 1969; soil and litter fauna, Chapman & Webb, 1978) on heathlands in southern England. The succession of spiders over ten years on burnt heathland was investigated in stands of different ages by Merrett (1976). He found a clearly-defined succession species on heathland regenerating after burning which depended on changes in vegetation structure and microclimate. The diversity of periods at which different species reach maximum abundance shows the importance of maintaining a mixture of different aged stands by rotational burning.

9.6.4 Timing and frequency of management

The effects of a particular treatment applied at one time of year will seldom be equivalent to the same treatment applied at an equivalent time of year. Traditionally, most methods of management are applied at particular times of year because they have been derived from agricultural practices which have had nothing consciously to do with conservation. Thus, mowing tends to be done in early summer and burning in late autumn or spring whilst grazing must be practised at all times of year (Morris, 1971b).

Short intensive periods of grazing have been shown to have important effects on leaf-miners and Heteroptera (Brown *et al.*, 1990). Seasonal grazing was shown to have adverse effects on Heteroptera and Auchenorrhyncha, when compared to no treatment and spring and summer grazing were more deleterious than autumn and winter grazing (Morris, 1973). The timing of cutting management has considerable effects on Hemiptera and Coleoptera. A field experiment in which cutting in May, in July, and a combination of both, was compared with an uncut control showed that a July cut reduced species richness and diversity of the Auchenorrhyncha fauna more than a May cut (Morris, 1981a, b; Morris & Lakhani, 1979). This was not true for Coleoptera (Morris & Rispin, 1987) which showed more variable effects (Morris & Rispin, 1988).

Chapter 10 General conclusions, predictions, management recommendations and future research

This final chapter links together the previous chapters. Initially, it provides an overview of the relationships between climate (change), vegetation structure, microclimate, flora and fauna (section 10.1). It then attempts to make certain predictions regarding the effects of climate change on British vegetation (principally on grasslands and heathlands) and its associated fauna (section 10.2). These provide directions for the future management of British habitats (e.g. within nature reserves) both generally, and separately, for grasslands and heathlands (section 10.3). Finally, in order to determine the effects of future climatic changes on the flora and fauna, lines of research are suggested to increase understanding of the microclimatic relationships described above, to monitor changes resulting from global warming and to test recommended changes in conservation management (section 10.4).

10.1 General conclusions

Certain conclusions can be made regarding the impacts of climate change and its influence on the flora and fauna (section 10.1.1). These effects can be interpreted in terms of the detailed effects of microclimate (section 10.1.2), vegetation structure (section 10.1.3) and their interactions (section 10.1.4) on understorey established vegetation, seedling regeneration and invertebrates (section 10.1.5).

10.1.1 Climate change

a) Global warming

Global temperatures reached their highest levels in the 1980s which included many of the warmest years. It is widely believed that 'global warming' is the result of the 'greenhouse effect'. Levels of carbon dioxide (CO_2), the main 'greenhouse gas' which absorbs infra-red radiation, are increasing markedly due to the burning and decomposition of fossil fuels and tropical forests. Elevated CO_2 has effects on plant physiology and development including altered photosynthetic rates, water-use efficiency, stomatal density, growth, flowering and seed production and differentially favours certain plant species (e.g. C_3 over C_4). Recent climate models predict a general warming of the earth's surface, particularly at higher latitudes and in winter. This is likely to increase precipitation by up to 10% due to greater evaporation from the sea and land and may also increase the

frequency of extreme climatic events such as fires, hurricanes and droughts.

b) Climate change effects

i) Plants

The distribution of many plant species in Britain is largely determined by climatic variables which limit their ability to disperse. Species with a pronounced northern distribution are largely remnants from pre-glacial time. These are amongst the most endangered members of the British flora. Many plant species are restricted to the south of England by a requirement for higher summer temperatures which limits plant development and seed production further north. If the climate changes radically, profound effects can be expected on the native flora. These effects will appear as changes in the timing of seed germination and flowering in response to drought, extremes of winter and summer temperature and changes in the length and distribution of the growing season. Likely consequences are the northern expansion of species with a predominantly Mediterranean distribution, recession of species with a northern distribution, extension of lowland species to higher latitudes, and a retreat of upland and montane species. The rate of vegetation change will be closely related to the lifespan and population dynamics, of component species, e.g. dispersal and germination strategies.

ii) Invertebrates

The majority of invertebrate groups occur in the south of Britain where the climate is mildest and would be expected to expand their ranges. However, northerly distributed and montane species are especially at risk, the latter particularly because their move to higher altitudes would not be matched by the extent of their habitats. Many soil organisms have wide ranges of tolerance of temperature and moisture and short-life cycles which permit rapid genetic adaptation (but see Gange & Brown, 1990). Climate change, as predicted, is unlikely to have dramatic effects on this component. Soil processes, such as hydrology, decomposition and weathering, are predicted to change particularly on the free-draining soils of the south and east which would become more like those of warm temperate and Mediterranean areas (i.e. more droughted). This means that the associated biota will be more likely to change on the free-draining soils of the south and east than on the heavier, more waterlogged soils of the north and west. This may be particularly crucial for lowland heathlands

since the most diverse and interesting communities occur on the more peaty soils.

10.1.2 Microclimate

The maritime, temperate (macro-) climate of Britain shows no extremes of heat, cold, flood or drought, but the north tends to be cooler, wetter, more windy and less sunny. However, differences may occur in relation to altitudinal, maritime and topographic influences and on a more local (microclimatic) scale between north- and south-facing slopes. Microclimate describes the 'boundary layer' where the influences of soil, vegetation, slope and aspect are strongest. Vegetation creates its own 'ecoclimate' which on the smallest scale, measured in mm, e.g. a leaf surface, is referred to as the 'nano-' or 'epiclimate'.

10.1.3 Vegetation structure

Vegetation structure defines the vertical arrangement of biomass which describes vegetational complexity. Distinct vertical layers occur within terrestrial habitats, namely, the sub-soil, rock, top-soil, ground zone, field layer, low canopy, high canopy and air above vegetation. Changes in vegetation structure include fluctuations, periodicities, regeneration and succession. Successional changes occur in plant and animal communities, for example, in terms of patterns of species composition, diversity and life-history strategies, associated with major changes in the environment. Abiotic factors (e.g. fire, drought, wind, soil fertility, topography, slope and aspect) and biotic factors, (e.g. seed rain, seed banks, and grazing by large herbivores and phytophagous insects) affect germination, plant performance and reproduction and thereby determine vegetational composition and structure.

10.1.4 Effects of vegetation structure on the fauna

Effects of vegetation on associated organisms are two-fold. Firstly, there are the direct microclimatic effects already discussed, and secondly, there are the direct mechanical effects which regulate the distribution of resources for feeding, resting, egg-laying etc. Most insect herbivores are highly selective in their feeding, choosing only certain plant species and tissues. As well as microclimate, host-plant selection is limited by physical problems of attachment, nutritional problems of plant-feeding and the presence of secondary plant compounds. Plant species composition is often a more important determinant of some insect herbivores communities than plant structure (e.g. weevils, leaf miners). However, for other herbivorous

insect and carnivorous invertebrates (e.g. spiders), plant architecture has a greater influence on community structure.

There is often a relationship between the structural diversity of a plant and the richness of its insect fauna, particularly in the later stages of succession. Larger, more complex plants, like trees and shrubs, provide more microhabitats and support a richer fauna than small, simple plants, like herbs and grasses. In heathlands, spatial and architectural diversity increases with stand age (i.e. phase) and is significantly related to insect species richness. Faunas may differ between seedlings and adult plants. As well as community patterns, changes in several life-cycle strategies of insect herbivores, such as generation time, wing polymorphism and overwintering stage, can be related to changes in habitat structure, while others such as reproductive potential and niche breadth are a direct result of changes in plant species composition.

Vegetation structure has an important influence on web-site selection and species composition in spider communities (e.g. limestone pavements, forest plantations) as demonstrated experimentally. Web-builders, which occupy sites that differ in structure, may have access to different prey types and sizes. In most cases, vegetation structure may have a more important influence than microclimate or prey availability, although these are inextricably linked. Likewise, the species composition and density of bird communities often increases with vegetational heterogeneity. Breeding bird populations change in relation to the developmental age of woodland. Studies in a range of temperate and tropical habitats such as grasslands found that bird species diversity could be predicted in terms of the height profile of foliage density and is usually unrelated to plant species diversity.

10.1.5 Vegetation and microclimate

All plant surfaces develop a boundary of relatively still air where winds have little effect and where temperature and humidity can be markedly different from ambient. Generally, the temperature excess on a leaf is greater at the centre than the margin and on upper compared to lower surfaces. However, microclimates vary between plants largely due to variations in the size, shape, reflectance, texture and orientation of their leaves and flowers. Temperature, light regime, wind and moisture conditions are all modified under the canopy, litter, bryophyte layer and this affects the bryophytes, lichens, small surface animals and flora and fauna of the soil surface. Vegetation types vary in their albedos (or reflectance of radiation) and this greatly determines the microclimates which are possible.

a) Grasslands

Microclimatological profiles in grassland have shown that stratification of air temperature is related mainly to that of radiation. Sunshine penetrates the upper region, but there is often a considerable fall thereafter and practically no direct insolation at lower levels. Humidity increases near ground level, particularly if there is a well-developed litter layer. The depth of light penetration depends upon the height, density, and mode of growth of the sward and the sun's height, which all vary diurnally and seasonally. Unlike agricultural grasslands, semi-natural grasslands exhibit more horizontal heterogeneities (e.g. tussocks) which due to their greater density and height reduce fluctuations in the lower part of the vegetation much more markedly. This greater vegetational complexity has significant effects on the associated fauna.

b) Heathlands

In heathlands, temperatures are lower and humidity greater beneath the canopy of heather plants than in the air above. This is more marked on calm and sunny days compared with windy, dull days. Structural changes occur in heathland vegetation which profoundly alter microclimate. Plants grow from seedlings, become larger and more woody, occupy more space and show changes in aerial structure associated with variations in green matter and litter production. This affects light penetration and thereby the germination and establishment of seedlings and the occurrence and distribution of many animal species. Where there is a constant pressure from factors which prevent scrub development and maintain open heathland, cyclical processes operate consisting of four phases: pioneer, building, mature and degenerate. The more open pioneer and degenerate phases have more extreme microclimates, whereas the dense canopy of the building and mature phases profoundly modifies this pattern by reducing illumination, restricting air movement and intercepting precipitation.

10.1.6 Microclimatic effects

In order to understand the detailed effects of climate change on the flora and fauna, it is necessary to examine the detailed effects of microclimate. This is particularly true in the case of invertebrates, whose distribution is largely limited by water loss.